THE RELATION OF THE MADREPORITE TO THE PHYSIOLOGICAL ANTERIOR END IN THE TWENTY-RAYED STARFISH, PYCNOPODIA HELIANTHOIDES (STIMPSON).*

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Ten Figures in the Text.

In a previous paper ('18) the writer recorded some facts concerning the bilateral tendencies and habits in *Pycnopodia helianthoides*. These were based on data gained from experimental studies and on others from observations on the behavior of the organism in its native environment. It was the writer's purpose at that time to follow the paper of 1918 with one on the physiology and histology, as well as other structural features of this species, and for this reason certain points were omitted from the paper mentioned above which might well have been included therein. Owing, however, to the writer's remoteness from the Pacific coast for the last five years and the lack of material on which to conclude this second work, it has been quite impossible for this additional contribution to appear sooner. During the last summer (1921) the writer was, however, so fortunate as to find opportunity to visit Puget Sound and gather some additional information on *Pycnopodia*. (It may be of interest to note in this connection that the transplantation of *Pycnopodia* from Bremerton to West Seattle was successful, which was shown by the fact that specimens of various sizes were found on September 2, 1921, on the piles under the docks at West Seattle, where about 12 specimens were planted in the spring of 1915, notwithstanding the difference in salinity at these two places. It was impossible, on account of lack of time, to determine whether the specimens found at West Seattle, 1921, were the same as those planted there in 1915, or whether they were the progeny of the latter. *Vide* Kjerschow-Agersborg, 1918.) From the additional data gathered this summer (1921) it is possi-

* Contributions from the Zoölogical Laboratory of the University of Illinois, No. 197.

ble to conclude this paper, although in an abridged form.

Investigators do not agree in regard to the position of the madreporic plate in Asteroidea. Ludwig ('99), dealing with the genus *Asterias,* says:

"Falls wie es, trotz der nicht seltenen Ausnahmen die Regel ist, nur eine einzige Madreporenplatte vorhanden ist, liegt sie stets im vorderen linken interradius, wenn man den Seesterne bei abwärts gerichtetem Munde mit dem Interradius des Afters nach vorn stellt," p. 540.

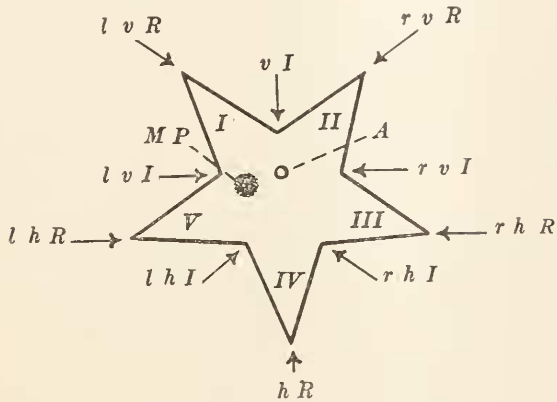

Fig. 1. A copy of Ludwig's figure of the asteroid groundplan, showing Ludwig's morphological "anterior" end. (P. 537.)

A, anus; *h.R,* posterior radius; *l.h.I,* left posterior interradius; *l.h.R,* left posterior radius; *l.v.I,* left anterior interradius; *l.v.R,* left anterior radius; *M.P,* madreporic plate: *r.h.I,* right posterior interradius; *r.h.R,* right posterior radius; *r.v.I,* right anterior interradius; *r.v.R,* right anterior radius; *v.I,* anterior interradius.

Agassiz ('77) claims that the madreporite is always in the suture of the terminal arm of the pentagon, which brings it opposite the third arm. This is also the view of Bury ('95). Rathbun ('87) says it is generally placed about midway between the center and the margin of the disk, and Sedgwick ('09) records that the madreporite varies in number in various species of starfish.

Delage and Hérouard ('03) say: "Elle est située dans la région apicale, tout près de la centro-dorsale, dans un interradius autre que celui qui porte l'anus. Le madréporite détermine une deuxième symétrie bilatérale, mais qui est altérée par l'anus, comme celle qui dépends de l'anus est altérée par le madréporite.

"Quand on regarde l'animal par la face dorsale, l'interradius madréporique vient après l'interradius anal, séparé de lui, d'un côté, dans le sens indirect (inverse de celui de la succession des heures sur un cadran), par un seul interradius, de l'autre par deux interradius," p. 2.

". . . quand on regarde l'animal par le pôle apical, l'anus est en arrière, le madréporite en avant et à droit," p. 3.

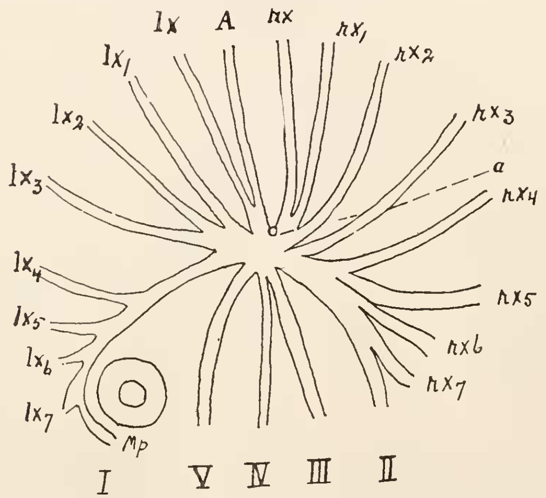

FIG. 2. Ritter's and Crocker's figure of the dorsal radial muscles of *Pycnopodia helianthoides,* showing the relation of the radial muscles to the asteroid groundplan, as represented in Fig. 1. *A,* the "anterior" ray; I-V, the "posterior" rays; rx–rx_7, rays added, on the right side, to the original six rays after metamorphosis; lx–lx_7, rays added to the left side; *a,* anus; *Mp,* madreporite.

Shipley ('93), MacBride ('96), and Lankester ('00) do not commit themselves in regard to the position of the madreporite, *i.e.*, as far as the starfish is concerned.

Ritter and Crocker ('00) in their work on *Pycnopodia* adopted Ludwig's and Agassiz's plan of numbering the radii of the typical five-rayed echinoderm. According to this, when the apical side is uppermost, counting from the madreporite clockwise, the rays are numbered from I.–V. These authors go on by saying: "From a study of the metamorphosis, Ludwig, '82, considers that the star should be oriented by a line running interradially between I. and II. and radially along IV., thus bringing the madreporite in the left anterior interradius" (Fig. 1).

"Before Ludwig was consulted, this orientation had been adopted for *Pycnopodia*, owing to the striking bilateral symmetry displayed in the young animals. This symmetry determined that the sixth ray is median anterior between I. and II., and by us has been called "*A*" (Figs. 4, 5). Ritter and Crocker's diagram (Figs. 4 and 5) agree with Ludwig's (Fig. 1). The relative position of ray "*A*,"

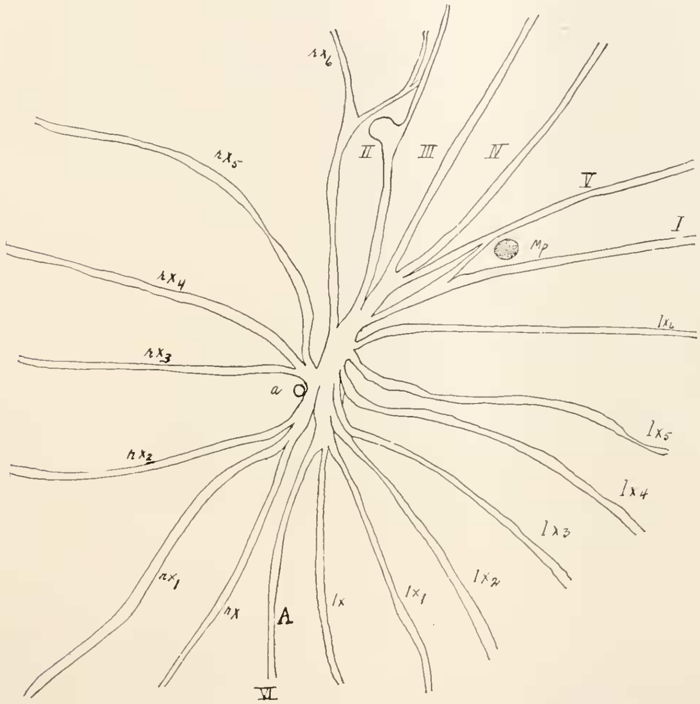

FIG. 3. A diagram of the dorsal radial muscles of *Pyncnopodia helianthoides* to show the relation of the primary and secondary rays to the physiological anterior end. (Rays I, lx_6, lx_5, lx_4. lx_3, correspond to I, V, IV, III, II (Fig. 2) respectively); rays I–V, rays of the physiological anterior end; these rays, and ray *A*, are, perhaps, the primary rays; rays lx–lx_6, the secondary rays of the left side; rx–rx_6, the secondary rays of the right side correspondingly; rays rx_6, and lx_6, the youngest rays. *a*, anus; *Mp*, madreporic plate. This sketch is made from the under side of the dorsal muscles.

in *Pycnopodia*, according to Ritter and Crocker, to the five rays of the asteroid ground plan, is between the left and right anterior rays (Figs. 1, I.–II.; and 4, I.–II.); the axis of bilateral symmetry, or Ludwig's orientation line, lies along rays *A*–IV. (Fig.

4), or along a line drawn between vorderer Interradius-hinterer Radius (Fig. 1).

Delage and Hérouard claim that the relation of the madreporite is far from being precise, and their orientation of the asteroid plan corresponds to Ritter and Crocker's figures of young individuals, if they be inverted. This is true, however, only in a general sense for the madreporite which comes on the right side, but the anus is placed in the same relative position in either case. This relation is different in the adult. Here the madreporite is on the left anterior side between the rays I. and V. and actually corresponds to Ludwig's plan. But the so-called five primary rays of Ritter and Crocker, which, according to Ludwig ('99), correspond to 3–IV.,

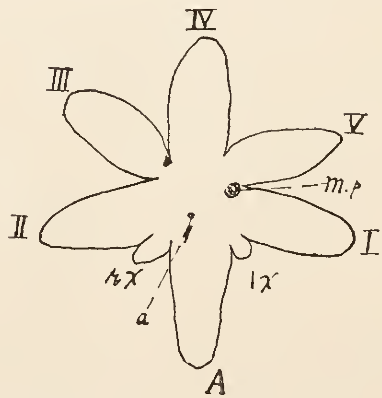

FIG. 4. Young individual, aboral view, in the eight-rayed stage (from Ritter and Crocker); the sketch is inverted to show the probably anterior rays (I–V) and their relation to the madreporite and the anus, *mp*, *a*, respectively. *A*, the posterior primary ray. (Compare this figure with Figs. 6, 7, 8, 9). The labeling is retained as in the original.

2–III., 1–II., 5–I., 4–V., respectively (Fig. 6), for the larva and the ground-plan of the common starfish, are not the posterior rays in adult life of *Pycnopodia,* however, but the anterior rays. This is easily seen in an actively moving individual, and may also be readily learned from the study of the interpolation zones which lie between rays II.–VI., VI.–I. It seems quite reasonable that the movements of *Pycnopodia* should be in the direction of, or along the axis of, the oldest rays, with the oldest rays as determiners of direction of movements. For, as I have shown before ('18), this starfish does not only move with the same side all the time as anterior end, but its speed is considerably greater than that of the common star; its highest speed, *e.g.*, when moving to deeper water during the receding tide, was 122.5 cms. per minute. Opposite to the largest number of rays, in early post-larval life, is one ray, which is perhaps of the same age as the other primary rays, and with this single ray are young ones, varying in strength and age. As a matter of fact, it should be expected that if there are any distance receptors at all, which act as influencing factors on behavior, they would be present in the earliest developed tentacles. This seems to be probable in *Pycnopodia:* It always moves at right angles to the zones of radial growth; the anterior end in adult life, being always the side which possesses the fewest, but uniformly sized, rays anterior to the radial interpolation zones; *in young specimens the number of the large rays is greater for the anterior end.* In adults the number of the anterior rays is five; and the youngest of all rays is a pair, one on each side of rays II. and I.; the number of rays of the posterior end varies with the total number of rays. In living animals it is quite easy to distinguish between the ages of the rays. There is a gradual increase in size of the rays posteriorward from the interpolation zones, the youngest being, of course, found at the latter points. This seems to indicate that the so-called posterior end is the physiological anterior end.

Kjerschow-Agersborg ('18) demonstrated experimentally that out of 50 righting reactions of *Pycnopodia,* 46 were toward the anterior end with an average speed of about 57.1 sec. per normal turn. In this species a physiological anterior point is actually established (*vide ut supra et infra*), the anterior ray is ray IV.; the madreporite holds the relation as indicated by Ludwig, Agassiz, Ritter, and Crocker for the five-rayed starfish (Figs. 1, 4, 5, 6, 7).

It may be noted that in Ritter and Crocker's diagram (Fig. 2) the anus is in front of the base of the radial muscles, according to the interpretation of these writers; but by the establishment of the physiological anterior end the anus comes nearer the posterior end than before, while the madreporite is placed nearer the anterior end. This, however, does not change their relation to the respective rays, but the relation remains the same as before. That is, the madreporite is still in the interradius V.–I. of Ludwig. The position of the anus, in fact, corresponds, now, with Delage and Hérouard's asteroid plan. Figure 2 is copied from Ritter and Crocker ('00) and represents a diagram of the muscles of the aboral disk, seen from the inside, and as though looked down upon, showing the apical radial muscle bands, the madreporite, and the position of the anus close to the origin of the muscle of ray *A* (VI.). If ray *A* were the anterior end, then the anus would be anterior to the center of the dorsal side; but since ray *A* is, in fact,

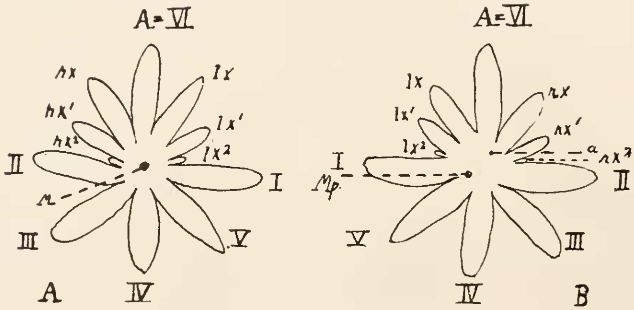

FIG. 5. Young individuals in the 12-rayed stage to show the interpolation zones: rx^2–lx^1. These figures are as per the original and show the reverse condition as in Fig. 4, which has been inverted to show the right relation of the madreporite to the true anterior end. *A*, oral view; *B*, aboral view. (From Ritter and Crocker.)

the posterior ray, the anus becomes placed posterior to the mid-dorsal point. Delage and Hérouard ('03) adopt Cuénot's plan ('91), with the madreporite in the interradius III.–II.; the anus in interradius II.–I., a little posterior of the mid-dorsal, but also a little to the right of the median line (Fig. 9). This seems to be an arbitrary matter of orienting the star. If the interradius I.–II. of Cuénot is placed as anterior end, the anus comes in the similar position as in Ludwig's plan: the madreporite is in interradius II.–III.; the anterior end is ray III. (Fig. 9). My drawing of the radial aboral muscles does not correspond at all with Ritter and Crocker's, in the point of orientation, and, in fact, also in the points relative to the general radiation of these muscles. I have compared the arrangement of the apical radial muscles in both large and small individuals having the same relative number of rays and have found them to be exactly as represented in my sketch (Fig. 3). I can not accept Ritter and Crocker's orientation represented in their sketch (Fig. 2); but even if their interpretation should be correct, and indeed it may be for young individuals, *it does not hold for adults relative to their physiological anterior end.* Rays II., III., IV., V., I. represent the anterior end in respect to progressive movements of the starfish in its native environment (Fig. 3). The figure here is inverted, *i.e.,* the madreporite should face the reader on his left side; the sketch is made from the inner side

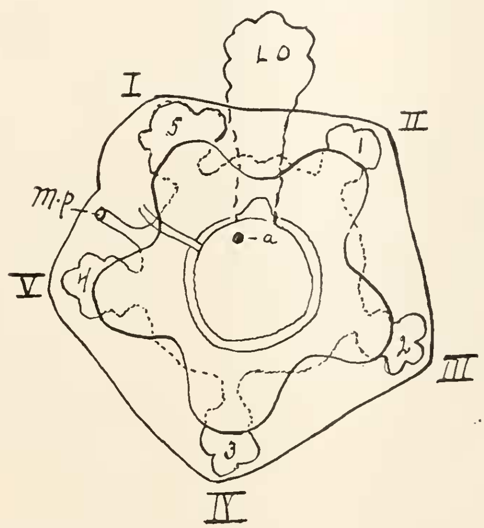

FIG. 6. Diagram of the asteroid groundplan of the metamorphosing common starfish. 1–5, radial vessels (larval); I–V, adult radial vessels; *a,* anus; *Lo,* larval lobe organ; *mp,* madreporite. (From Ritter and Crocker.)

of the aboral disk, looking down upon it. I am not concerned, at this time, about the controversy I may be led into relative to the difference between Ritter and Crocker's diagram and their interpretation and my diagram; I am only recording facts relative to the physiological anterior end in *Pycnopodia helianthoides* (Stimpson), and I am trying to adjust myself as far as possible with the accepted view in this field of morphology. In my opinion, the apical radial muscles of *Pycnopodia,* relative to their axial arrangement to the physiological anterior and posterior ends, fit in very well with the marked bilaterality of the adult, as I have recorded elsewhere ('18). The radial symmetry is, indeed, superimposed.

Cole ('13) demonstrated with marked clearness, experimentally, what Cuénot and Delage and Hérouard had demonstrated morphologically, viz., that ray III. is the anterior ray. Cole, from his experiments on *Asterias forbesi,* constructs a line of bilateral symmetry with regard to his records; an approximately equal number of trials fall on each side (Fig. 8). A line drawn perpendicular

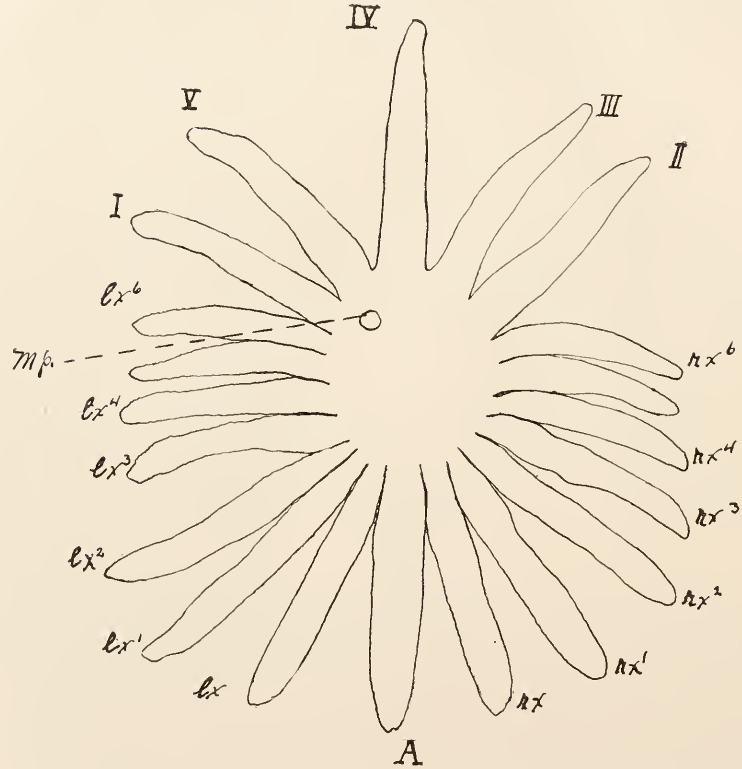

FIG. 7. Diagram of an adult individual of the twenty-rayed starfish to show the bilateral appearance in an individual actively moving about, and the relation of the madreporite (*mp,*) to the physiological anterior end (rays I–V); and of the anus (*a*) to the rest of the dorsal disk. *A*, primary posterior ray. rx–rx^6, the oldest and youngest right post-larval rays; lx–lx^6, oldest and youngest left post-larval rays.

to the line of bilateral symmetry, intersecting mid-dorsally, brings out of the total number of 499 trials: 347 ahead of it, *e.g.,* on the side which bears the madreporic plate; 152 behind, or to the side which bears the anus. Ray IV. records 107 trials, ray III. 137, and ray II. 103 trials out of the total of 499; while rays V. and I. have only 74½ and 77½, respectively. This is, indeed, a very striking contrast to Ludwig's so-called "vorderer Interradius," *e.g.*, interradius I.–II., the *ipso facto* posterior end. If the physiological anterior rays of *Pycnopodia are in fact the morphological anterior rays,* as represented by Ritter and Crocker (although theirs must be inverted), then all facts agree. (Compare Figs. 2, 3, and 7.) In *Pycnopodia* the line of bilateral symmetry lies along

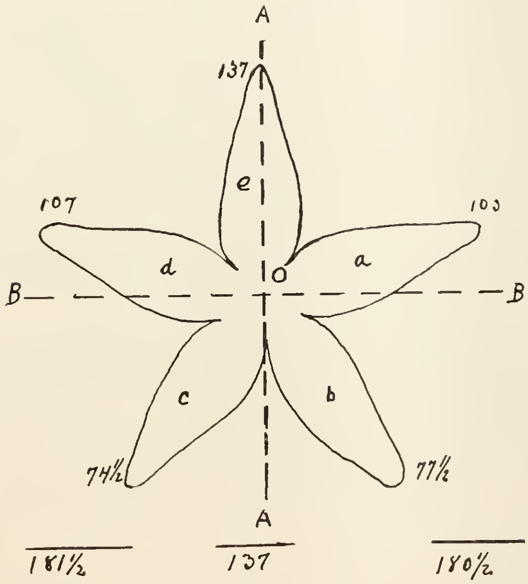

FIG. 8. Diagram to show the physiological anterior end of *Asterias forbesi,* and its relation to the madreporite. Line *AA,* plane of bilateral symmetry; *BB,* dissects the star into an anterior and posterior pole according to direction of locomotion. The *number* at the end of each ray indicates the exact number of attempts the star used that ray as "anterior" ray in locomotion; ray *e,* is seen to have the largest number in its favor. (Ray *e* = III, Cuénot.) The sum of the trials indicates a "right" and "left" which correspond very well to a plan of bilateral symmetry. (From Cole.)

the rays IV.–*A* (ray *A* = VI.); this is explainable by the fact that five of the six primary rays become the anterior rays, with ray IV. in the lead, and rays III., II. on the left, and V., I. on the right (Fig. 7). The relation of the madreporite and of the anus to the dorso-radial muscles is then demonstrated (Figs. 2 and 3). Ray

A (or VI.) is the median posterior ray (Fig. 7), while ray IV. is in the lead. Figs. 4 and 5 show the relation of the madreporite to the physiological anterior end in young specimens of *Pycnopodia;* the apical ray, *e.g.*, ray IV., is uppermost on the page (Fig. 4). In Fig. 5, *A* represents the oral view. Ritter and Crocker accepted as anterior end that pole of the star which corresponds to the larval lobe organ (Fig. 6, *Lo*), but if the physiological anterior end in *Pycnopodia* corresponds to the posterior end of the common starfish, then the larval lobe organ has nothing to do with it, at least not in *Pycnopodia.* It is, of course, an open question whether the anterior rays (II., III., IV., V., I., Fig. 3) correspond to the posterior rays of the same numbers in Ritter and Crocker's sketch (Fig. 2). If they do not, then the physiological anterior end in the adult *Pycnopodia* has become established independently of the factors as noted above. But this may not be the case. Of course,

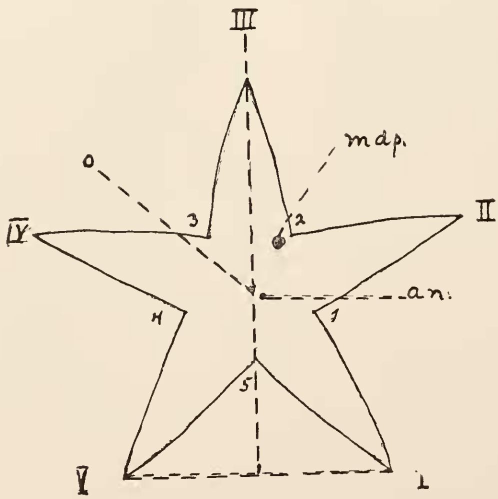

FIG. 9. Diagram to show the morphological groundplan of the common starfish. III, anterior end; *an*, anus; *mdp*, madreporite; *o*, morphological center; 1–5, interradii; I–V, radii. (From Delage and Hérouard.)

the common starfish may indeed move with any of its rays in the lead (Jennings, '07, p. 155); and "do the same thing, under the same conditions, in a number of different ways, and never do the same thing twice in exactly the same way" (Coe, ('12)). The anterior ray of these species of starfish (*Asterias forreri, A. for-*

besi, and *A. vulgaris*) has not been easy to determine in the adult. Although Dr. Cole, as we have seen, comes nearest to establishing an anterior pole in the five-rayed starfish, *A. forbesi* (Fig. 8). Jennings ('07), in experiments on righting reactions, also found that: "Individual starfish do have a more or less permanent 'set' toward the use of a certain ray in pulling themselves over in the

Fig. 10. Photograph of a small specimen of *Pycnopodia helianthoides* with 14 rays. Notice five rays on one side, and two on the opposite side, are regenerating from autotomy. *Rps*, respiratory papillæ. Natural size. Photo by author.

righting reactions." *A. forreri* uses the same ray (*e.g.*, ray *e*, *vide* Fig. 8) that *A. forbesi* uses as anterior pole. This anterior pole seems to be directly homologous with the anterior end in *Pycnopodia*, judging the size of the rays and their relation to the smaller ones in the latter.

The number of madreporites, especially in multiradiate species, may vary: Cuénot ('91), Ludwig ('99), Delage et Hérouard ('03), Sedgwick ('09), Verrill ('14), Crozier ('21), and on that account the true position of the madreporite is difficult to determine. In a few cases I have found the madreporic plate present on the right anterior nearly opposite the base of ray V., but I have never found more than one in *Pycnopodia helianthoides*. Crozier ('21) records asexual reproduction in *Coscinasterias tenuispina* (Lamk.), its model number of rays in the adult being seven, and that, together with this method of autotomous multiplication, madreporites are also multiplied at separate points on the disk: "an assurance that portions of the body separated by autotomy will each be provided with a madreporite." He abandons the notion which he held at first, that "There is a physiological basis for the development of one or several madreporites according to the number of rays, *i.e.*, depending on the total water requirements of the locomotive organs." *Pycnopodia*, a much larger species (even though the ray lengths in the two species may be the same, *Pycnopodia* is larger in bulk than *Coscinasterias*, because it has about three times more rays than the latter), and with a locomotive speed about nine times greater than *Coscinasterias*, has usually only one madreporite. That is, it gets along with only one. Sometimes autotomy is practiced in *Pycnopodia* (Fig. 10), but not for the purpose as recorded by Crozier for *Coscinasterias*. Verrill ('14) reports a multimadreporic case for *Pycnopodia*, but he considers that to be abnormal. It seems, therefore, that while the anterior end in *Pycnopodia* is much the same as in the common starfish, the position of the madreporite on the dorsal disk may vary. But it is always nearer the physiological anterior end. Crozier also finds this to be true for *Coscinasterias*. The fact that *Pycnopodia* is bilaterally symmetric even after metamorphosis (no one has seen the larva of *Pycnopodia*, but it is assumed that it is bilaterally symmetric as in other echinoderms) may be a factor which aids it in the development of a locomotive speed greater than that of other starfish, and that it consequently "selects," by means of the law of least resistance, the oldest and most efficient pole as anterior end. This pole, judging from the relationship which the smallest rays bear to the physiological anterior end, is at right angles to the two interpolation zones, the zones of the least locomotive efficiency during the postembryonic development. Ludwig's asteroid ground-plan, applied to the ordinary starfish, does not hold completely for the twenty-rayed starfish; his "vorderer Interradius" becomes the "hinterer Interradius." The physiological anterior end corresponds more nearly to Cole's finding for *Asterias forbesi*, viz., that part in proximity to the madreporite is the anterior physiological end, the madreporite being on the left anterior side.

Summary.

1. The physiological anterior end in *Pycnopodia helianthoides* corresponds to the posterior end of Ludwig's ground plan for *Asterias.* The anterior end possesses a relatively larger number of old (large) rays in early life than it does in late life. The new rays are added at two interpolation zones posterior to rays II., I.

2. The madreporite is, as a rule, on the left anterior side; it varies in position, but it is always found on the anterior part of the dorsal disk, *i.e.*, at the base of rays III., IV., or V. The so-called five primary rays (Ritter and Crocker), which, according to Ludwig, correspond to 3–IV., 2–III., 1–II., 5–I., 4–V., respectively, are not the posterior rays in adult life of *Pycnopodia*, but the anterior rays. Ray IV. is the anterior ray in adult life.

3. The establishment of the physiological anterior end in *Pycnopodia* shows that the madreporic plate is anterior to the mid-dorsal and the anus posterior; this arrangement agrees fairly well with Delage and Hérouard's plan for the five-rayed starfish. It also corresponds with Cuénot's plan for the common starfish, with Jennings's "more or less permanent 'set,'" and with Cole's "physiological anterior"; it is the reverse of Ludwig's asteroid ground-plan relative to the numbering of the rays.

Acknowledgments.

The writer wishes here to express his indebtedness to Professor Trevor Kincaid, of the University of Washington (Seattle), for his ever-ready assistance and financial aid in the collection of the data for this and the previous paper (1918) on *Pycnopodia;* to Professors H. B. Ward and H. J. Van Cleave, of the University of Illinois, for criticizing the manuscript of this contribution.

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